THE PRINCIPLES OF GEOGRAPHIC DISTRIBUTION AS APPLIED TO FLORAL ANALYSIS

HERBERT L. MASON

In attempting to analyze the present flora of California in terms of its history and floristic relationships many problems of interpretation and procedure present themselves, which call for a study of the dynamic processes that have governed the distribution of plants throughout the long history of the spermatophytes. The results of these studies have been the building up of certain dicta that seem for the present, at least, to serve as a working hypothesis from which strides can and have been made toward this original objective of the problem. Although this goal has not as yet been reached, it seems desirable to place on record at the present time the basic principles arrived at, that they may serve to stimulate discussion and thereby, it is hoped, clarify the point of view and bring to the subject the thoughts and opinions of others working in this field.

In the light of paleobotanical evidence, it is not possible to regard the flora of California solely as a phytogeographical unit occupying a biogeographical province whose major characteristics are largely the expression of the climatic differences of a varied topography. Instead, it must be regarded as the product of the bringing together and sorting out of many floristic units, derived from several sources, which have accommodated themselves to new social alignments which are expressed by the present flora of California as we now see it in more or less apparent climatic balance.

Proceeding on the assumption that floras in general are the product of complex processes of floristic evolution, we may attempt to analyze them in terms of their particular origins. This evolution of floras not only involves the organic evolution of morphological and physiological characters of the plants, but also the intricacies of migration. The climatic changes causing migration also bring about selection and segregation of species and permit the intermingling of previously unassociated plants. These intricate dynamic processes have so complicated the floras of the world that on the basis of the distributional features of the modern representatives of the floras alone any inferences as to their movements are likely to be superficial except in certain very obvious cases. Our most reliable source of information, however incomplete, is the fossil record left in beds whose position in the geological sequence can be correctly ascertained and correlated with other plant-bearing deposits. There must also be recorded in these deposits plants whose taxonomic status is unquestionably determinable, a problem increasingly difficult as we go backward into the geological record and one calling

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for extreme caution in its interpretation. Only then can we speak with any reasonable degree of certainty of the time and space sequence in the movement of floras and their significance in the interpretation of climate.

R. D'O. Good (3), dealing with the problems of angiosperm geography, outlined for this group of plants what he termed the "Principles" governing their distribution. He brought together, in a logical sequence, the obvious incontestable truths that have guided botanists in the past in their deductions but which had never before been assembled as a unified working hypothesis. The purpose of Good's work, as stated, was to arouse interest in the subject that we might construct a proper scientific foundation upon which to build our ideas of plant distribution. Good's principles, on the whole, need to be amplified to make them more precise in their application. They deal only with general dicta pertaining to the environment and to migration without considering adequately—except as the Theory of Tolerance might be applied—the responses of the plant and the perpetuation and evolution of floras. These subjects, in the opinion of the writer, are of sufficient importance to justify their inclusion in the principles of plant geography.

In the following pages there is recorded a series of principles, some of which are accepted as stated by Good, others are amplified to make their application more precise, while several new proposals are presented for the consideration of plant geographers. It is not intended that the problems of plant geography be considered as settled here; much cooperative thought and research must still be expended before even the basic principles of this vast subject can be expressed in final form. The present ideas are the results of ten years of study of the problems of distribution of the California flora and have been gained from observations of the modern plants and of the fossil records as they have revealed the story of the migrational history and floristic evolution of the component parts of this flora over an area extending from Point Barrow, Alaska, to Mexico, and eastward through the Rocky Mountains, a region containing one of the most complete Tertiary plant records available to the world.

The principles here presented are organized under four headings. The first deals with the general subject of the environment in a dynamic sense, including the factors of the environment and the physical basis for their modification and control. The second group deals with the responses of the plant as governed by the Theory of Tolerance and the Principle of Limiting Factors. The third group is concerned with migration and establishment, and the fourth group deals with the perpetuation of vegetation and the evolution of floras. The word distribution is used herein only to imply the area of occupancy and not dispersal.

I. The Environment of the Plant

1. *Plant distribution is primarily controlled by the distribution of climatic factors and in any given region the extremes of these factors may be more significant than the means.*

This is a restatement of Good's first principle with the limitation clause involving the extremes added. That plant distribution is primarily controlled by climatic factors seems obvious when considered in terms of the floras of the various climatic zones. That the extremes of climate are more significant than the means may require an explanation. The occasional year or occasional season, wherein a critical factor is in excess of the tolerance of a species for that factor, often demonstrates in a striking way the importance of the extreme as a limiting factor in distribution. For a long time we were puzzled by the failure of the redwood to move northward into what appeared to be a favorable terrain. There seemed to be little in the way of climatic factors operating to prevent it, since trees transplanted, even as far north as British Columbia, grew well.

In the winter of 1932 abnormally low temperatures were experienced in California. McGinitie (6) observed that throughout the northern range of the redwood all the new growth was materially affected by freezing. These low temperatures are much more prevalent in the coastal regions to the north and although the mean varies little northward, such extremes are reached often enough over a period of years to prevent establishment and hence migration. This is clearly a case of the extreme being the controlling factor. W. P. Taylor (8), in dealing with problems in zoology, as they were observed to affect distribution and functioning during the cold winter of 1932 on the one hand and the drought of the summer on the other, noted the imporance of this factor in conjunction with a critical time. Taylor was impressed by the effects of extreme climatic conditions which are wholly abnormal and which occur rarely to occasionally. He noted that such occurrences had very profound biological effects and in some instances wiped out certain species or so weakened them that they were the ready prey of their enemies. According to Taylor, the importance of these extremes necessitates a restatement of Liebig's law (4) so as to bring in a concept of the critical time. His rewording of Liebig's law is as follows, "The growth and functioning of an organism is dependent on the amount of the essential environmental factor presented to it in minimal quantity during the most critical season of the year, or during the most critical year or years of a climatic cycle."

2. *Plant distribution is secondarily controlled by the distribution of edaphic factors.*

Obviously such control of distribution as is exercised by edaphic factors is conditioned by climate, both in respect to aerial climate and with respect to the climatic factor in soil decomposition and upbuilding. The achievement of the climax vegetation in the succession of a hydrosere or a xerosere is accomplished by the progressive subjugation of the original edaphic complex. Even in such highly specialized cases as large areas of serpentine outcrops with their specially adapted species, the vegetation must first be in accord with climate. It is, therefore, logical to place the edaphic factor as subordinate to the climatic factor.

3. *There has been great oscillation and variation in climate, especially in the higher latitudes during the geological past.*

Whether or not one agrees with Chamberlain (1) in his theory of the alternation of cool, dry, zonal climates and wide-spread, moist, humid climates, the fossil record reveals that many floras have occupied in the past different positions from those which they now occupy. The Cretaceous floras suggest wide-spread uniformity from Greenland in the Arctics to Graham-land in the Antarctics. This does not necessarily prove the absence of zonal climate in the world during this time but it does demonstrate a general rise in temperature, so that vegetation of an ecological type now confined to a region much farther south was permitted far to the north, as well as to the south of the equator. Climate seems to be the only significant variable that operates from one region to another in a manner which would stimulate the migration of floras.

4. *At least some, and probably considerable, variation has occurred in the relative distribution and outline of the lands and seas in geological past.*

Here again, in spite of debatable theories of horizontal earth movement, the evidence for elevation and subsidence is so strong as to be almost incontestable. Whether one accepts the theory of continental drift of Wegener (9) or adheres strictly to the older ideas of the permanence of ocean basins, concepts of the incursions of epicontinental seas are not materially affected. Both theories permit them and the evidence for their existence and the areas of their occupation is just as convincing in the light of either theory.

This principle, as well as the one dealing with climatic change, provides the mechanism for the control over the climatic and edaphic factors, throughout time, as well as the means for the establishment and removal of barriers to migration.

II. The Responses of the Plant

To understand the workings of geographic principles, it is necessary to go back to the fundamental physiological processes as they apply to the individual plant. The plant as an organism behaves strictly in accordance with orderly physiological laws. The factors of the environment must, in the last analysis, be interpreted in their effect on specific physiological processes. The physiology of plants is governed, first of all, by the laws of evolution and genetics in delimiting their potential behavior. The range of this potential behavior is the measure of the plant's plasticity or variability, and limits the nature of the responses to varying stimuli. It is in physiological response that we find the mechanism for most of the processes of plant distribution and floral evolution. It is, therefore, important that they be considered in the theories of plant geography.

5. *The functions governing the existence and successful reproduction of plant species are limited by definite ranges of intensity of particular climatic, edaphic, and biotic factors. These ranges represent the tolerance of the function for the particular factor.*

This statement accepts the major thesis of Good's Theory of Tolerance and the Theory of Physiological Limits proposed by Livingston and Shreve (5). It seems better in the generalized statement, however, to restrict the concept of tolerance to a specific tolerance of a specific function, as is done in the Theory of Physiological Limits. The sum of tolerances does not serve a useful purpose; neither is the total span of the tolerances of the various functions for a factor necessarily significant. The most significant tolerance range is the intensity span of the factor during any particular phase of development from the maximum of the critical function having the lowest maximum, to the minimum of the critical function having the highest minimum for the particular factor. This span might be taken as the range of tolerance of the plant for this particular factor, but during this phase only. During another phase of development, the span of tolerance may be either lessened or broadened at one or both of its extremes. This leads directly to the principle of limiting factors, which when applied to plant geography, may be stated as follows:

6. *In the life history of the organism there are times when it is in some critical phase of its development which has a narrow tolerance range for a particular factor of the environment. The distribution of this intensity span of the factor during the time the plant is in this particular phase limits the area in which the function can operate and, hence, governs the distribution of the species. The narrower the range of tolerance, the more critical the factor becomes.*

When we consider the large numbers of seeds that fall in an area and germinate and the small number that establish themselves at least to the point of entering into competition, we may conclude that establishment is a critical phase not only in migration but also in the life history of the individual. The high percentage of elimination of migrules during this critical period suggests that the tolerance range for the factor controlling this establishment is very narrow. So long as the intensity of this factor remains within the range of tolerance of the species, the plant will become established so far as it is influenced by this factor. If the intensity exceeds the tolerance of the species, establishment will fail, and this factor becomes a limiting one in this phase of the plant's development. With establishment effected, this particular range of the factor is no longer critical or limiting. It is probable that the factors limiting establishment are among the most important of climatic barriers and certainly they play a prominent part in preventing the spread of many exotic species introduced by man. Often in California orchards, fruit is not set when the blooming period coincides with rains or heavy fog. These factors may become limiting because the excess moisture may destroy the pollen or the cloudiness and fog may so retard the activities of insects as to prevent pollination. The blooming period then is the critical phase in the production of fruit. Cloudiness and fog and the same degree of moisture excess are not limiting to other phases of the plant—they may even stimulate them to higher development. Therefore, with respect to these factors, the critical phase of the plant is significant.

III. Migration of Floras

Since it is apparent that migration has been an agent in the development and evolution of floras, it is important that this process have a place among the principles of plant geography.

7. *Great movements of floras have taken place in the past and are continuing to take place.*

The most convincing evidence of past migration of floras is the history of the flora that has been associated with the record of *Sequoia sempervirens*. In tracing the history of redwood in North America, it is necessary to go more deeply into the geological sequence as we go northward. We find it in the Eocene of Alaska and Canada, the Oligocene of Oregon, the Miocene of California and Nevada, and the Pliocene of California, where it became restricted to its present coastal distribution by the close of the Pleistocene. The conclusion is evident that as time progressed, the redwood and its associates moved farther and farther southward.

The revegetation of the glaciated areas of Northern and Eastern North America and the slow retreat of modern glaciers with the populating of the areas they occupied afford evidence that floral migrations are still in progress.

8. *Migration is brought about by the transport of individual plants during their motile dispersal phases and the subsequent establish*ment *of these migrules.*

Migration is not merely the dispersal of seeds or other migrules. It is not effected until establishment is complete, and establishment, since it is limiting to migration, becomes, therefore, the most critical phase of the process. It is necessary then to modify Good's principle involving migration to include the establishment phase of the problem. The mechanism behind the establishment is the mechanism of stimulus and response wherein particular factors of the environment act upon particular functions of the plant.

IV. The Perpetuation and Evolution of Floras

Were it only the environment and the control exercised over it by diastrophism and subsequent climatic change that played a part in vegetation, extermination of all plants would have been accomplished long ago. The plasticity of the plant species, as well as its mobility, have enabled vegetation not only to persist but to become so modified that one may well speak of such a phenomenon as the evolution of floras.

9. *The perpetuation of vegetation is dependent first upon the ability of the species to migrate and secondly upon the ability of the species to vary and to transmit the favorable variations to their offspring.*

The great oscillations of climate that have occurred in the past caused the species of plants making up the vegetation either to migrate or to adjust themselves to the new conditions; plants failing to do this became exterminated. All three of these processes have played a part in the development of vegetation on the earth.

The palaeontological record contains much evidence of migration, organic evolution, and extermination. The result has been an ever changing floristic scene in the geological past, leading up to the development of the present floras. This brings us to a consideration of the principle governing the evolution of vegetation.

10. *The evolution of floras is dependent upon plant migration, the evolution of species, and the selective influences of climatic change acting upon the varying tolerances of the component species.*

Migration as an agent of floristic evolution functions to bring to any region a stream of new floristic elements, that adapt themselves to the forces causing the migration with the result that a new association is developed. On the other hand, migration may carry a flora up against an impassible barrier and cause its extermination. The extermination of one species from a society of plants opens the area for the development or expansion of other species; this results in a change in the aspect of the association.

The ability of species to adapt themselves to the changed conditions is perhaps a measure of their vigor, and the more vigorous species are the more rapidly evolving. Thus, these vigorous species, by extending their tolerances and perhaps also undergoing morphological change, are introducing new plant elements into a floristic association.

The selective influence of climatic change causes some species to migrate, others to become extinct, and may well be an activating influence in the evolution of species. That such processes have been working in the past may be demonstrated by what appears to have been the nature of the origin of differentiation of certain elements of the Sierran flora of California from the Tertiary redwood flora.

A large number of Sierran species are endemic to the California flora. This is particularly true of the flora of the middle altitudes where *Pinus Lambertiana* and *Libocedrus decurrens* occur. Associated with these species are a great many plants which also occur with the redwood forest. This is especially true in the northern Sierras where the flora bears a striking resemblance in its species content and general aspect to the flora of the Coast Ranges. There is, however, no redwood.

The Sierran flora as we know it does not occur in the fossil record. In every case, species belonging to it are found in close association with the redwood. In the Santa Clara lake beds of the Pliocene (2), for example, the pine and *Libocedrus* are in association with *Sequoia* and *Pseudotsuga*. In the older Tertiary beds to the north there are five-needled fascicles similar to those of *Pinus Lambertiana* although otherwise there exists no proof of the close relationship of this pine to the modern species.

Libocedrus is of frequent occurrence in the Miocene and Oligocene. These Sierran types increase in abundance in the redwood flora up through the Pliocene, then they segregate out following lines based on relative humidity. Those tolerating arid conditions develop along the Sierra Nevada range and the removal of the formerly dominant species from the flora allows the other species to expand and take over the dominance of the forest. In the South Coast Ranges the arid phase found opportunity for some development, but is losing ground and in certain areas such as the Santa Cruz Mountains, where it formerly occurred, it is almost extinct. The sugar pine and incense cedar no longer occur there although they were present in the Pliocene.

Along with this selection it seems probable that some evolution took place. This must have involved particularly the tolerance of some of the species. There seems no other logical way of explaining the former association of species whose descendants are now living in areas controlled by different temperature and moisture ranges. How else can we explain the association of *Sequoia, Taxodium,* and *Ginkgo* in the Miocene?

Should our deductions relative to the origin of the so-called "Californian" element of the Sierran forests prove correct, we can explain the redwood element in the northern portion of it as a relict flora located near the original point of divergence in a region where the Sierra Nevada and Coast Ranges merge in the North. If the Sierran forest had a separate existence in the Tertiary it seems that some evidence for that fact would be found in the abundant Tertiary deposits of Western North America. However, its records are always in association with the redwood flora. The diminishing abundance, in progressively older Tertiary beds, of forms closely related to modern species, is very instructive and points to the rise of a group of species destined through the agency of climatic selection and segregation to develop a new flora.

Further evidence of climatic segregation was pointed out by the writer (7) in outlining the history of the Monterey flora wherein the splitting up of a uniform Pleistocene flora into two descendants with differing climatic requirements was pointed out. Such selective influence, no doubt, plays a part in the history of the development of related discontinuous floras the world over.

Discussion. We can, therefore, expect to find in any particular region evidence that the flora had a polyphyletic source. In California, we have a large number of plants whose history is associated with the immigration from the north of the redwood, and out of this migrating flora several of the major plant associations of Western America were segregated. There is a large element in the California flora that has adapted itself to the changes attendant upon the southward movement of the redwood. This element was the flora of the Tertiary Archipelago of California, which had a maritime phase restricted to the windward side of the islands and an arid phase occupying the leeward side of the islands much like the modern flora of Cedrus Island. This arid phase extended southeastward on the continent toward the plateau region of Mexico. The non-adaptive elements of this flora were segregated far to the southward and survive in the plateau regions of Mexico. From this southern region in Post-Pleistocene time, attendant upon the amelioration of climatic conditions, there is evidence of another migration proceeding northward and some conspicuous elements of our flora can be traced to these areas. The details of these migrations are in the process of being assembled and before long we shall have enough material for a reasonably complete account of their history.

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LIGNIFICATION OF XYLEM FIBRES IN PARKINSONIA ACULEATA

Flora Murray Scott

Parkinsonia aculeata,[1] one of the palo verdes of the southwestern desert, is commonly cultivated in Los Angeles County, and in the Palm Springs region. It is a handsome tree, freely branching, with a wealth of yellow flowers in early summer (5). The formation of cork is confined almost entirely to the main trunk, which, in consequence, alone lacks the gay green color to which the palo verde owes its name.

Microscopic examination of the switch-like stem reveals such obvious xerophytic characters as the heavy cutinization of the persistent epidermis, the sunken stomata, the presence of a hypodermal layer of water-containing cells, and the development of a photosynthetic cortex. A striking feature of the stem is the abundance of starch throughout the completely lignified xylem.

The present paper is concerned with the development of the starch-containing fibres which make up the bulk of the xylem tissue.

Observations

In the xylem of *Parkinsonia*, seasonal rings are well marked, and the wood is made up of the following elements: tracheal tubes, fibres, and medullary rays. No unlignified, thin-walled xylem parenchyma was noted in the differentiated stems. The fibres are of the type termed "substitute fibres" by Eames and MacDaniels (4), i.e., living fibre elements which function in food storage. In *Parkinsonia* occur two types of substitute fibres which

[1] Correction: in a previous paper by the author, "The anatomy of *Cercidium Torreyanum* and *Parkinsonia microphylla*" (Madroño 3: 33–41. 1935), for *Parkinsonia microphylla* read *Parkinsonia aculeata* in the title and throughout the article.